A PRELIMINARY COMMUNICATION UPON THE CEREBRAL COMMISSURES OF THE MAMMALIA,

WITH

SPECIAL REFERENCE TO THE MONOTREMATA AND MARSUPIALIA.

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(Plate xliv.)

"The subject requires careful re-investigation, but if the currently received statements are correct, the appearance of the 'corpus collosum' in the placental mammals is the greatest and most sudden modification exhibited by the brain in the whole series of vertebrated animals—it is the greatest leap anywhere made by Nature in her brainwork."—*Huxley*, "Man's Place in Nature."

The cerebral commissures of the non-placental mammal present a simplicity of arrangement, which may be readily understood, so that a study of their distribution is likely to throw a considerable amount of light upon the more complicated systems of connecting fibres in the brain of the placental mammal. The knowledge of the arrangement of the commissures of the Proto- and Metatherian cerebrum, moreover, must have an important bearing upon the proper understanding of the morphology of the brain of all sub-mammalian Vertebrates, since the Monotremata and Marsupialia form the connecting links between the latter and the higher mammals. This tracing of the homologies with the Eutheria is all the more important because the common descriptive terms have mostly been originally applied to parts of the higher mammalian brain, especially that of the Primates.

During the present year, acting upon the suggestion of Professor Wilson, to whom I am deeply indebted for much valuable advice, I have examined a considerable number (about thirty) brains of the Monotreme and Marsupial orders, more especially those of *Ornithorhynchus* and *Perameles nasuta*. A knowledge of the gross anatomy having been obtained by dissections of fresh brains, the minute anatomy was worked out in serial sections of the whole brain cut in coronal, sagittal and horizontal planes. The Weigert-Pal and Golgi staining methods were used for most of the work, supplemented by occasional use of anilin blue black. In addition to the above, the cerebrum has been examined in the Phalanger, *Macropus*, Koala, Kangaroo-rat, *Dasyurus* and *Echidna*, and compared with those of the rabbit, pig, cat, dog, guinea-pig and mole. From a series of fœtal specimens of *Phalangista* of various ages, I was enabled to make out many points in the cerebral development. Through the kindness of Professor Wilson and Mr. J. P. Hill, I was enabled to examine some beautifully stained series of sections of fœtal Kangaroos and Bandicoots, as well as a very valuable series of sections of a fœtal Platypus, whose external appearance is described in this number of the Society's Proceedings. For the abundant supply of material with which this research was conducted, I am deeply indebted to Dr. C. J. Martin, Mr. J. P. Hill and Dr. Meredith, of Raymond Terrace. To Mr. Robert Grant I am under a deep obligation for much valuable assistance in the histological work.

In the Marsupial and Monotreme brain the greatest interest centres in the unique arrangement of the cerebral commissures, the uniformity of whose general plan throughout these orders indicates the close relationship between the Proto- and Metatheria, and separates them as a distinct and well defined group from all the Eutherian orders.

This paper is merely intended as a synopsis of that part of the subject which relates to the commissures. The complete results of the work on the non-placental cerebrum I hope to present to the Society in a short time.

At an early stage in the development of the non-placental mammal, the mesial wall of the prosencephalic vesicle becomes indented to produce two parallel furrows, in exactly the same way as occurs among the Eutheria. The lower of these two furrows, which extends forwards as far as the foramen of Monro and backwards as far as the posterior extremity of the lateral ventricle, is the *fissura choroidea.* The upper corresponds to what has been called the *fissura arcuata (Bogenfurche* of Arnold) in the placental mammal and is coextensive with the lateral ventricle. Included between these two fissures is a strip of cortex, which is known as the *arcus marginalis (Randbogen)*, which (owing to the deficiency of the cortex lining the fissura choroidea) becomes the edge of the cortex cerebri. The fissura arcuata of the Monotreme and Marsupial brain differs from the corresponding structure in the placental mammal, in that it persists into adult life as the fissura hippocampi in the whole extent of the ventricle, thereby meriting the name of "*Ammonsfurche*" given to the corresponding structure in the Eutherian brain by Mihalkovics. In the non-placental mammal, then, the hippocampal fissure forms a projection —the hippocampus—into the lateral ventricle in its whole extent. The fissure, and consequently the hippocampus, corresponds in shape with the contour of the ventricle. So that in Platypus, where the lateral ventricle has only a small descending horn (so small that it was quite overlooked by Hill, "On the Cerebrum of Ornithorhynchus," (Philosophical Transactions B. 1893), the hippocampus and hippocampal fissure present a slight hook-like bend downwards at their posterior extremity. This is shown in a somewhat exaggerated manner in fig. 2 *hf.* In all Marsupials the fissura hippocampi (fig. 1 *hf.*) presents a well marked curve downwards at the posterior extremity corresponding to the downward curve of the lateral ventricle to form its descending horn. From the arcus marginalis is formed the fascia dentata and from the projection into the ventricle the cornu Ammonis, whose histological structure closely resembles that of the corresponding regions of the Eutherian brain, as described by Ramon y Cajal.*

* "Neue Darstellung vom histolog. Bau des Central-nervensystems," Archiv für Anat. p. 377, 1893.

The ventricular aspect of the hippocampus is covered in its whole extent by the alveus, a layer of fine medullated nerves, which arise as axis-cylinder processes of the large pyramidal cells of the hippocampus (especially those near the fimbria) and from the polymorphous cells, which form the nucleus fasciæ dentatæ. "Collaterals" derived from the same sources also pass into the fimbria to become "commissural" fibres. All these fibres converge towards the thickened lamina terminalis, which is the homologue of the *septum lucidum* of higher Mammals. In order to reach this point, above the foramen of Monro, the fibres coming from the anterior extremity of the hippocampus are directed backwards and inwards, and those coming from the posterior part of the hippocampus are directed forwards and inwards with varying degrees of obliquity. Since the greater part of the entire hippocampal formation is placed behind the foramen of Monro, including the whole of the descending horn, which alone is present in Eutheria, there is, consequently, a large mass of fibres coursing forwards and increasing as it goes, from fresh accessions of alveus fibres. This mass of fibres becomes collected to form a distinct ridge which constitutes the *fimbria*, which is mainly derived from the descending horn. The fimbria, therefore, will vary in size with the length and degree of development of the hippocampus behind the foramen of Monro, more especially with the size and extent of the descending limb of the hippocampus. In Platypus, and to a less marked degree in *Echidna*, the descending part of the the hippocampus is short, and in neither is the layer of alveus fibres thick in this region. As a consequence neither Monotreme has a well-formed fimbria. In all Marsupials, however, there is an extensive part of the hippocampus lying posterior to the foramen of Monro and a well developed descending limb, so that the cut fimbria projects as a prominent spur in transverse section. Since the hippocampus extends forwards beyond the foramen of Monro, no part of the fimbria ever becomes free from the hippocampus to form posterior pillars or body of the fornix as in placental mammals. The fimbria, or its representative, lies in the whole of its extent along the margin of the cortex, where that is formed by the fascia dentata. The latter structure in Platypus throughout forms the upper border of the choroid fissure, but in *Perameles* and others, where the ventricle turns downwards, and the descending cornu thus formed bends forwards, the fascia dentata and fimbria come, of course, to occupy a position at the *lower* margin of the choroid fissure in its descending limb, and the fimbria lies *above* the fascia dentata in this region. The destination of the alveus fibres, after they have arrived at the region of the foramen of Monro, varies.

(*a*) The great majority of the fibres cross the middle line to enter the hippocampal region of the opposite side, so that they effect an exchange of fibres between the two hippocampi. In the alveus of the opposite hippocampus they give off numerous collaterals which enter the white matter and come into relationship with the pyramidal cells. These fibres constitute therefore the *hippocampal commissure* proper of Owen and Symington—the *corpus callosum* of Flower, Sander, Osborn and almost all recent writers—the *hippocampal decussation* (in Platypus) of Hill. Its origin from cells of the hippocampus (including the subiculum and fascia dentata) indicates without the slightest possibility of doubt its homology with the psalterium of Eutheria.

(*b*) A large bundle of fibres dips downwards behind the anterior commissure to enter the optic thalamus. This is the *anterior pillar of the fornix.*

(*c*) A third smaller and more scattered bundle arches forwards in the mesial wall of the hemisphere in front of the anterior commissure—the *precommissural fibres of Huxley.*

(*d*) A considerable number of alveus fibres pass into other regions of the same hippocampus from which they arise. These may be called *hippocampal association fibres.*

The present paper will only deal with the first of these sets of fibres—the hippocampal commissure—and will only refer to the others in so far as they are related to the commissural fibres. It may be remarked, however, in passing, that Hill's statement* that "all such fornix as exists in *Ornithorhynchus* crosses in the middle line" and that the descending fornix fibres come from the hippocampal commissure is absolutely erroneous, since the great majority of such fibres come directly from the alveus and never cross the middle line. His further description of their destination and of the formation of the taenia thalami is equally inaccurate.

On separating the cerebral hemispheres of any Marsupial or Monotreme from above, a large white transverse band will be noticed passing between the two hemispheres and hiding from view the anterior extremity of the third ventricle and the foramina of Monro. The question of the homology of this band has been the subject of much controversy.

A full account of the earlier discussion of this question will be found in the paper of Flower,† and the more recent bibliography will be found in the papers of Symington‡ and Hill.§ Ever since Meckel's monograph|| there have been supporters of his view that the superior commissure was corpus callosum. Thus Flower in *Echidna* and a series of Marsupials,¶ Pappenheim in *Didelphis*,** Sander in *Macropus* and *Didelphis*,†† Osborn in fœtal *Macropus*,‡‡ Zuckerkandl in Platypus,§§ and Herrick in *Didelphis*,|||| as well as in numerous papers elsewhere, have, among others, supported

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* *Loc. cit.*

† "On the Commissures of the Cerebral Hemispheres of the Marsupialia and Monotremata," Phil. Trans. 1865, p. 633.

‡ "The Cerebral Commissures in the Mammalia and Monotremata," Journ. of Anat. Vol. xxvii. p. 69.

§ "Cerebrum of Ornithorhynchus," Phil. Trans. B. 1893.

|| Descr. Anat. Ornithor. parodoxi, 1827.

¶ *Loc. cit.*

** Compt. Rendus, Vol. xxiv. p. 186, 1847.

†† "Ueber das Quercommissurensystem des Gehirns bei den Beutelthieren," Arch. f. Anat. 1868.

‡‡ "The Origin of the Corpus Callosum," Morph. Jahrbuch, Vol. xii.

§§ "Ueber des Riechcentrum," 1887.

|||| "Callosum and Hippocampus in Marsupial and lower brains," Journ. of Comp. Neurology, Vol. iii. p. 179.

the view of Meckel that a corpus callosum is present. Haeckel as recently as 1893 has made use of the following terms in describing the essential features of the Marsupial and Monotreme brains. Among the "Hereditiv-charactere der Monotremen" he places "die primitive reptilienähnliche Bildung des Gehirns, insbesondere der Mangel eines ausgebildeten Corpus Callosum," and referring to the Marsupialia, "die geringe quantitative und qualitative Entwickelung des Gehirns, namentlich des Corpus Callosum."* Beevor, who, after an examination of the cerebrum of *Macropus*, expressed the opinion that the superior commissure was corpus callosum (Brain, 1887), elsewhere denies the presence of any hippocampal commissure in certain Primates.† Apart from the evidence of the presence of such a commissure which the non-placental mammal affords, there is the valuable corroborative evidence of its presence in the placental mammal by Honegger.* The opinion of Owen that the corpus callosum is absent in the Non-placentalia is supported by Eydoux and Laurent,† by Robert Garner in Platypus and several Marsupials,‡ by Symington in the clearest and best account of the subject which has yet appeared,§ and Hill;|| and Edinger in the fourth revised editions of his lectures¶ says that all Marsupials so far examined lack a corpus callosum.

In spite of this the generally accepted opinion among recent writers [of which, for instance, the works of Foster and Balfour, as well as the more recent work of Minot on Embryology and the

* "Zur Phylogenie der Australischen Fauna," Jena.

† "On the Course of the Fibres of the Cingulum, &c., in the Marmoset Monkey," Phil. Trans. 1891.

* "Vergleichend-anatomische Untersuchungen über den Fornix, &c.," Recueil de Zoologie Suisse, Tom. v. Nos. 2 and 3.

† "Sur l' Encephale de l'Echidna comparé à celui de l'Ornithorhynque," Voyage de la "Favorite."

‡ "Anatomy of the Brain of some small Quadrupeds," British Assocn. Reports, 1858, p. 123.

§ *Loc. cit.*

|| *Loc. cit.*

¶ "Vorlesungen über den Bau der Nervösen Centralorgane," Leipsig, 1893.

comparative papers of Sir William Turner,* may be quoted as examples] is that all mammals possess a corpus callosum. This opinion is still actively upheld by Herrick in his numerous papers, although in a different (but equally mistaken) sense to all other writers. So that to-day there is still considerable uncertainty upon this question, in spite of the short but clear and convincing paper of Symington.†

So far no attempt has been made to explain either the arrangement of the fibres in this commissure or the difference in shape which it presents in different animals, and which so deceived Flower. This paper aims at offering an explanation of these appearances.

If a sagittal section be made through the mesial wall of the cerebral hemisphere of *Perameles*, *i.e.*, a short distance from the mesial plane of the brain, the section stained by Pal's method presents an appearance which is represented in a purely schematic manner in fig. 1. In the middle of the figure is seen the section of the commissure (*ps.*), which has given rise to so much discussion, and radiating from it the fibres (*f.*) of the alveus are schematically represented proceeding to all parts of the hippocampus, whose contour is represented by the hippocampal fissure (*hf.*) From the concavity of the hook formed by the commissure are to be seen issuing the fibres of the anterior pillars of the fornix (*af.*) and the precommissural fibres of Huxley (*s.*) separated by the anterior commissure (*ac.*).

In fig. 2 the corresponding structures in *Ornithorhynchus* are represented in a similarly schematic manner. The psalterium or superior commissure here presents only a slight hook at its posterior extremity corresponding to the rudimentary posterior descending cornu of the hippocampus. Consequently the commissure is not folded in bilaminar form as it is in *Perameles*. In fig. 3 the condition found in the placental mammal is diagrammatically represented.

* "The Convolutions of the Brain," Journ. of Anat. Vol. xxv. 1890; "The Cerebrum of *Ornithorhynchus*," Journ. of Anat. Vol. xxvi.

† *Loc. cit.*

In *Perameles* the sagittal section of the commissure is thin in front, where it is composed of scattered bundles coming from the anterior part of the hippocampus. But as it is traced back it becomes thicker and more compact from the crowding together of fibres from the middle portion of the hippocampus. Posteriorly the commissure takes a sudden bend downwards and forwards, and at the bend a large number of fibres are aggregated to form a structure which resembles the *splenium corporis callosi* of placental mammals, and was actually believed by Flower to be the splenium. Since it is produced in the same manner as the splenium, it may not be inappropriate to call it the "*splenium of the hippocampal commissure.*" From this splenium the ventral limb of the commissure extends downwards and forwards like the psalterium of the placental mammal, and as in the latter it is formed mainly by the fimbria. In the higher Marsupials the angle formed at the splenium by the two layers of the commissure becomes more acute, and in the highest Metatherians like the Kangaroo the two layers form two parallel bands united behind at the splenium. After this description of the arrangement in *Perameles*, the appearance of the commissure met with in Platypus will be readily understood. As the descending horn of the ventricle is rudimentary there is a very small descending limb of the hippocampus. There is consequently no ventral layer of the commissure, but only a slight hook-like "splenium" at the posterior extremity of the commissure. In the Eutheria (fig. 3) where that portion of the hippocampus lying above the velum interpositum does not develop, there is consequently no *dorsal* layer of the hippocampal commissure; but, corresponding to the ventral part of the hippocampus, which alone persists, the ventral layer of the hippocampal commissure forms the psalterium, as we usually understand that term—*the place of the dorsal layer of the commissure being occupied by the corpus callosum.* The corpus callosum of higher mammals is continuous with the psalterium at the callosal splenium, and the exact point of union of the two is not usually evident. Although in the highest mammals the splenium is formed wholly of callosal fibres, yet in some of the lowlier Eutheria, *e.g.*, *Mole* (Ganser*) it is formed of psalterial fibres, and is not therefore strictly a splenium *corporis callosi*, but corresponds rather with the "splenium" of the marsupial commissure. Ganser, from such considerations, and recently Paul Martin† from a study of the development of the corpus callosum in the cat, have come to the conclusion that the separation of the psalterium from the corpus callosum is purely artificial and serves no useful purpose, since both commissures connect parts of the cortex cerebri. These writers therefore include both structures under the term corpus callosum, and divide it into dorsal and ventral layers. But as I have already pointed out, the superior commissure of Proto- and Metatheria is formed solely of fibres derived from cells lying in the hippocampal region. This in Eutheria is the only distinguishing feature of the psalterium, that it is formed of fibres whose "Ursprungzellen" lie in the hippocampus, as distinct from callosal fibres, which consist solely of axis-cylinders and collaterals of cells lying in the mantle proper. The whole superior commissure of the non-placental mammal is strictly homologous then with the *ventral* layer of the great cerebral commissure of the placental mammal, while the *dorsal* layer of the latter is a pallial commissure superadded to the ventral, and superseding the dorsal, layer of the hippocampal commissure present in the Marsupials and Monotremes. If then it be permissible to consider the ventral layer of the Eutherian commissure as truly corpus callosum, we must, of course, admit that the Proto- and Metatheria have a corresponding structure, constituting, however, a corpus callosum, none of whose fibres arise in the mantle proper and which is, therefore, not strictly comparable to the great white band seen on divaricating the hemispheres of a higher mammal. This relationship of the superior limb of the hippocampal commissure in the Metatheria was not appreciated by Flower, who, from the resemblance of the whole commissure in sagittal section to the combined corpus callosum and psalterium

* "Vergleichend-anatom. Studien ü. d. Gehirn des Maulwurfs," Morph. Jahrb. Bd. vii. 1882.

† "Zur Entwick. des Gehirnbalkens bei der Katze," Anat. Anzeiger, 1894.

of Eutheria, regarded the dorsal layer of the marsupial hippocampal commissure as a true corpus callosum.

In the descriptions given above, I have described the appearance seen on section through the mesial wall rather than through the middle line, because in the latter plane the fibres have become collected into a more compact mass, and the simplicity of the arrangement is correspondingly obscured. It may be pointed out in this connection that the marked difference in the appearance presented on mesial section of, *e.g.*, such brains as those of *Echidna* and *Macropus*, are more apparent than real.

The mass of grey matter, which is situated on the ventral aspect of the hippocampal commissure in *Ornithorhynchus* and which fills up the concavity of the hook formed by the commissure in *Perameles*, is the homologue of the septum lucidum of Placentalia, being formed, like the latter, from the thickened lamina terminalis. The septum lucidum, therefore, in Marsupials (fig. 1) fills up the concavity of the "psalterial" hook, lying *ventral* to the dorsal limb or cornu of the hippocampal commissure, which alone is present in Platypus (fig. 2), *dorsal* to the ventral limb or cornu, which alone is present in Eutheria, while, as already stated, it lies in the Marsupial between the ventral and dorsal limbs of the commissures, which are both present. The septum lucidum, therefore, presents the same topographical relation to the corpus callosum of placental mammals as it does to the dorsal limb of the hippocampal commissure of non-placental mammals, so that Flower's* main argument for the existence of a corpus callosum—that it lies dorsal to the septum lucidum—loses all its cogency.

In this connection it is important to emphasize the fact that the "septum" lies entirely upon the ventral aspect of the hippocampal formation in Platypus and ventral to its anterior part in Marsupials. It lies, therefore, entirely *ventral* to the Randbogen, below which it is carried backwards with the superior commissure as the latter develops. Now the corpus callosum occupies the same position in relation to the septum pellucidum as the dorsal

* *Loc. cit.*

limb of the hippocampal commissure does in Marsupials, and develops in the lamina terminalis just as the corpus callosum does (Marchand, Paul Martin, Minot). Moreover the latter is continuous posteriorly with the psalterium. The corpus callosum from comparative reasons, therefore, as well as from the purely ontogenetic evidence in human brain by Marchand,* and Paul Martin in the cat,† lies entirely *ventral* to the Randbogen. Hill's statement‡ that "the corpus callosum in its backward extension breaks through a convolution, which lies outside the ring from which the fascia dentata, fimbria and fornix are developed," as well as the opinion of Fish "that in its dorso-caudal growth the callosum ploughs its way . . . through the arcuate gyre"§ are as equally opposed to the facts of comparative anatomy as they are quite unsupported by the brilliant results of Marchand's developmental researches.

Before a corpus callosum (using the term in the restricted sense in which anatomists generally regard it, *i.e.*, as distinct from the psalterium) can develop, either the hippocampus must disappear in the region in which the supraventricular callosal mantle-commissure is to develop, or the callosal fibres must traverse the hippocampal region. Of these alternatives the former is that which is found to take place. Accordingly in the ontogeny of the cerebrum of the placental mammal the anterior portion of the fissura arcuata (the "vordere Bogenfurche" of His), and consequently the hippocampal projection into the anterior horn and body of the lateral ventricle, disappears preparatory to the development of the corpus callosum, the "hintere Bogenfurche" alone persisting to become the hippocampal fissure, which forms a projection limited to the descending horn of the ventricle. This is quite in accordance with the belief of Professor D. J. Cunningham, who, as the result of his study of the development of the

* "Ueber d. Entwick. d. Balkens im Menschlichen Gehirns," Arch. f. Mikr. Anatomie, Bd. xxxvii. 1891.

† *Loc. cit.*

‡ "The Hippocampus," Phil. Trans. B. 1893.

§ "The Indusium of the Callosum," Journ. of Comp. Neurology, Vol. iii. 1893, p. 61.

human cerebrum, says*:—"I believe that it [vordere Bogenfurche] is transitory and that it is gradually obliterated during the time that the corpus callosum assumes shape." In Proto- and Metatheria the anterior commissure is the cerebral commissure *par excellence*, being the sole connection between all parts of the hemispheres, excluding the hippocampi only. It is of interest to note in this connection that the anterior commissure persists in Eutheria in just that part of the mantle related to the descending horn of the ventricle in which the hippocampus remains, while in the region from which the hippocampus has disappeared the anterior commissure is supplanted by the fibres of the proper corpus callosum. In the temporal lobe of Placentalia the alveus fibres (the root fibres of the hippocampal commissure) present the same relationship to the terminal fibres of the anterior commissure as they do to the same commissure in the whole range of the extensive hippocampal region of Non-placentalia. And, as the hippocampal region in the latter is co-extensive with the lateral ventricle, so the anterior commissure is co-extensive with the lateral ventricle, *i.e.*, supplies, in these forms, the whole of the cortex, excluding the hippocampus only.

The important question, "What is the significance of the corpus callosum?" must now be considered. Is it a new commissure to connect cortical areas hitherto unconnected or not present in lower mammals; or, on the other hand, is it merely a new path for fibres which possess representatives in the brains of the Meta- and Prototheria? From a consideration of the facts before us, it seems possible that the corpus callosum appears in response to the demand for a shorter connecting route between the rapidly developing dorsal portions of the cortex cerebri. That such factors are at work, the Marsupials themselves seem to afford evidence. In *Perameles* the anterior commissure passes around the corpus striatum as an external capsule to reach the various regions of the mantle. In *Phalangista*, a bundle of anterior commissure fibres proceeds to the cortex *vià* the internal capsule,

* Cunningham Memoirs of Roy. Irish Acad. No. vii. 1892, p. 5.

in addition to the external capsule. In *Macropus*, in order, apparently, to meet the demands of the greatly increased mantle, almost half of the anterior commissure fibres pass through the internal capsule to reach the dorsal part of the mantle. It seems as if this principle became extended in the placental mammal, and to provide for the enormous mantle development of the higher Mammalia, a shorter supraventricular route was established in place of the circuitous path, which the fibres of the anterior commissure would otherwise have had to take to reach such a region, for instance, as the callosal convolution in man.

Although from these considerations it seems as if the callosal fibres were serially homologous with the fibres of the anterior commissure, *i.e.*, fibres separated from the anterior commissure to meet the exigencies of a huge mantle-development, it must not be forgotten that the parts of the cerebrum which the corpus callosum connects, only develop late in the phylogenetic and ontogenetic history of the individual. Thus Sir Wm. Turner* states that the relative proportion of mantle to rhinencephalon decreases as we descend the Mammalian series until in the lowest mammals the pallium is almost as small as the rhinencephalon. In *Perameles* this reduction of pallium goes still further, as, instead of being as large as the rhinencephalon, the pallium forms merely a small cap placed upon the rhinencephalon. In the Eutheria a considerable portion of the mantle, viz., the temporal lobe, is connected by the anterior commissure. If, then, from the small cap of mantle found in *Perameles* we subtract the portion corresponding to the temporal mantle of higher forms, there will be little, if any, mantle left to be connected by a corpus callosum. In such higher Metatherians as the Wallaby the demand for a corpus callosum becomes greater, and is met to some extent by added fibres of the anterior commissure passing through the internal capsule. If in such a highly developed brain as that of the Wallaby, where the demand for a true corpus callosum is evident, such a structure is wanting, it seems *a priori* highly

* Journ. of Anat. Vol. xxv.

improbable that in the Sauropsida and Amphibia such a commissure should exist, as so many writers assert.

Although *a priori* statements are of little value as scientific argument, still with such presumptive evidence of the absence of a corpus callosum in Submammalia, one is naturally chary of accepting any opinion as to its presence, unless supported by definite and convincing evidence. Such evidence moreover is not yet forthcoming, and the arguments which have hitherto been adduced in support of the hypothesis, are of the flimsiest kind. Herrick states* "the callosum is practically absent [in *Didelphys*] . . . a rudiment of what may be called corpus callosum [is present], although we are unwilling to definitely homologise it with that body . . . it soon loses itself in the median walls of the hemisphere, corresponding to the septum pellucidum. Being a tract of cortex, this band has as great claim to be homologised with the corpus callosum as the relatively larger commissure of the alligator." The area which Herrick here calls "septum pellucidum" and elsewhere "intraventricular lobe" is an area of the mesial surface of the cortex, which is directly continuous posteriorly with the tract which has already been described as the septum lucidum and which develops from the lamina terminalis. The corresponding grey mass in Reptiles has been called "septum pellucidum" and "Fornix leiste" by Edinger† and Meyer,‡ although the latter would not definitely homologise it with the "septum" of Eutheria. Flower§ called it "septal area." All these terms are very misleading, because the area in question is not homologous with the septum lucidum, which is merely the thickened lamina terminalis.|| This tract, moreover, develops from the "posterior olfactory lobule" of His, and can be readily

* "Cerebrum and Olfactories of the Opossum, &c.," Bull. Sci. Laboratories, Denison University, Vol. vi. Part ii. p. 75.

† "Vergleichend-entwick. und anat. Studien im Bereiche der Hirnanatomie. 3. Riechapparat und Ammonshorn," Anat. Anzeiger viii. 10, 11.

‡ "Ueber das Vorderhirn einiger Reptilien," Zeit. f. wiss. Zool. lv. Bd. Nov. 1892.

§ *Loc. cit.*

|| Minot "Human Embyrology."

traced in the Mammalian series as the *gyrus subcallosus* of Zuckerkandl* or the "peduncle of the corpus callosum." Neither of these terms is applicable to the nonplacental mammal since there is no corpus callosum. The area in question may be distinguished as "*the precommissural area,*" a purely descriptive term equally applicable to all vertebrates possessing a cortex. The "precommissural area" from its connections and ontogeny is part of the rhinencephalon. Now the only two commissures which are known to have any connection with the rhinencephalon are the anterior and hippocampal commissures—the corpus callosum never. To distinguish some fibres of the hippocampal commissure by the name of "corpus callosum"—as Herrick does—simply because they go to the precommissural area is therefore entirely unwarranted, and opposed to all the accepted criteria of a corpus callosum. Since the corpus callosum of certain reptiles is confined to the homologous area, it is only natural to conclude that a corpus callosum is absent in them as it is in *Didelphys.*

Moreover, Osborn† in Amphibia speaks of a bundle of fibres as "a commissure of the dorsal portion of the mantle and homologous, on this ground, with the corpus callosum," quite oblivious of the fact that, by his own showing, the dorsal commissure in Marsupials is anterior commissure. Besides, Edinger‡ shows that the mesial and dorsal portions of the cortex of reptiles is homologous with the Ammon's horn, and therefore its connecting fibres must be hippocampal commissure. When it is upon such flimsy and unscientific evidence that many writers base their belief in the presence of a corpus callosum in Submammalia, one is fully justified in doubting their conclusions, especially when there is so much discordance as to what actually is the corpus callosum. Thus many writers (*e.g.*, Osborn, Gage, &c.) describe as corpus callosum a structure which is undoubtedly hippocampal commissure. Evidence is accumulating, which will go far to prove that the corpus

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* *Loc. cit.*

† *Loc. cit.*

‡ *Loc. cit.*

callosum of most writers on Submammalia, is nothing else than a hippocampal commissure—a view, which a comparison with the arrangement of the commissures in Platypus would lead one to expect. The great source of confusion to investigators not only upon the Marsupial but also upon the Sauropsidan cerebrum, in attempting to compare the latter with the placental mammal, is the altered position of the hippocampal commissure—firstly, by the bending of the hemisphere accompanied by a corresponding bend in the commissure, and secondly, the disappearance of just that part of the hippocampus and its commissure, which clearly maintains its true morphological position as the *upper* margin of the choroidal fissure, *dorsal* to the septum pellucidum. In the Platypus we have the key to unlock the whole question.

The following summary presents a hypothetical explanation of the presence and order of appearance of the three commissural bands met with in the region under consideration.

In the lowest stage of cerebral development the anterior commissure is the great commissural system of the cerebrum. Included in the anterior commissure are numerous strands of varied significance, which may in lowly forms be quite distinct from one another as they lie in the lamina terminalis, *e.g.*, in Teleostei, where this anterior commissure system is known as the "*commissura interlobularis*" (Göttsche). Early in development the upper border of the choroidal fissure becomes differentiated as a hippocampus, which, before the ventricle becomes bent, lies entirely dorsal to the fissure, as in Platypus and the Sauropsida. This is the portion of the cortex furthest removed from the situation of the anterior commissure, and hence this—the hippocampus—is the region which first demands a shorter route for its connecting fibres. Hence the hippocampal commissure appears as the second distinct commissural band, and we have the Monotreme and Marsupial condition.

In the ontogeny of the Eutherian brain this order of development of the commissures is also observed, the anterior commissure being the first to appear, and later the combined calloso-hippocampal commissure. Of the latter commissure, the commissural fibres of the fornix are the first to develop,* so that in the early Eutherian brain there is a stage which closely resembles the adult condition in Metatheria with "anterior" and hippocampal commissures and a complete absence of corpus callosum proper. Combined with this absence of the corpus callosum there is a persistence of the Bogenfurche, which completes the picture of the Marsupial brain, constituting a veritable "*Metatherian stage*" in the development of the Eutherian brain. These interesting facts in the development of the higher mammalian brain, which the recent work of Marchand and Martin have elucidated, fully bear out the statement of the late Sir Richard Owen that the hippocampal commissure in the Marsupials "represents the first stage of the corpus callosum as it appears in the development of the placental mammal"—a statement which has been repeatedly misunderstood by Owen's critics. The work of Owen, which was performed almost fifty years ago with the crude methods of investigation of that time, will stand the test of the latest methods of investigation which the last few years have yielded. In the light of our advanced knowledge of to-day, with all the delicate and selective staining agents and improved methods of research, the results of his labours on the brain of the nonplacental mammal stand out as a lasting memorial to his close observation and insight. The opposition which has been brought to bear against his investigations by so many prominent biologists, some of whom, from a less clear comprehension of the subject, attempt to depreciate the value and question the accuracy of his work, can have no other result than to expose their own ignorance. Even as late as last year, an English writer well known in neurological literature, in a disparaging attempt to find fault with Owen's work on Platypus, simply laid himself open to the accusations with which he ineffectually attempted to stamp the work of the great *savant*. The result of the present research on the cerebrum of a large series of Monotremes and Marsupials, with the methods of Golgi and Weigert, is to completely vindicate Owen from the

* Martin, *loc. cit.*

charges of inaccuracy which have been ignorantly levelled against him. I am well aware that the writer of the paper in question had very bad material with which to work, but that is all the more reason why he should have been more cautious in his attack upon others' work. The hypercritical tone of the paper in question reaches its acme in the following passages :—" On what ground, too, does Owen maintain, that the essential function of the fornix as a commissure . . . is maintained, when, as will be shown presently, *all such fornix as exists in Ornithorhynchus decussates in the middle line, is not united with the olfactory bulb and may be, for all one can tell to the contrary, not a longitudinal commissure at all, but a series of tracts uniting together corresponding parts of the two sides?* . . . "*He saw the difficulty, but not the way out of it.*"*

The closing phrase in this quotation accurately describes the position of its writer, who, by ignoring the close and intimate connection of the hippocampus with the olfactory lobe (the internal root, the *Riechbundel* of Zuckerkandl, and "the *olfactory bundle of the fascia dentata*" of the present writer), and having elsewhere stated that the external olfactory root cannot be traced to the hippocampus, completely excludes the hippocampus from any connection with the olfactory region, in spite of the fact that he correctly located the fascia dentata as the olfactory centre. But for the statement of Owen that the "association" between the olfactory and hippocampus is maintained to a greater extent (as compared with the commissural connection) than in higher animals, his statements may be taken as strictly accurate, a very close and intimate association existing between the anterior extremity of the hippocampus and the olfactory lobe, by means of fibres passing through the precommissural area, and which are probably homologous with some of the "precommissural fibres of Huxley" and the striæ Lancisii of the Eutherian cerebrum. The latter homology is rendered all the more probable by the statements of Blumenau† that the striæ Lancisii, which are continued pos-

* The italics are mine.

† *Loc. cit.*

teriorly into the fascia dentata, are connected anteriorly with the olfactory lobe, in much the same way as I have elsewhere shown my "*olfactory bundle of the fascia dentata*" to be connected in Platypus.

After the appearance of the hippocampal commissure the increased development of the mantle next demands a shorter course for its connecting fibres, which is provided by the corpus callosum. If these conjectures are right, the three cerebral commissures must be regarded as serially homologous, the anterior commissure, or at least its pars olfactoria,* appearing first, the hippocampal commissure next, and the corpus callosum last. That some of the fibres, which in Placentalia pass in the latter, cross the middle line with the anterior commissure in Non-Placentalia seems certain, so that part of the anterior commissure is really the homologue of the corpus callosum in the Proto- and Metatheria, the hippocampal commissure being merely a part of the anterior commissure, which has become separated off earlier in phylogeny. The appearance of a corpus callosum can hardly be considered then, therefore, such a sudden event as would appear at first sight and such as Professor Huxley's remark *(supra)* seems to imply, but is merely an example of the adaptive element in development, which recent research has recognised as the important modifying factor of phylogenetic tendencies in ontogeny.

What becomes of the anterior extremity of the hippocampus in the placental mammal? Comparison with the non-placental mammal supports the view, which is forced upon one by the important researches of Marchand† and Blumenau,‡ that the *gyrus supracallosus* of Zuckerkandl§ (the *indusium* or *striæ Lancisii)* is the representative of the anterior part of the hippocampus.

* The "pallial" part of the anterior commissure probably does not appear until after the hippocampal commissure.

† *Loc. cit.*

‡ "Zur Entwickl. v. feineren Anatomie des Hirnbalkens," Archiv f. Mikr. Anatomie, Bd. xxxvii. 1891.

§ *Loc. cit.*

In man and microsmatic mammals the temporal part of the hippocampus retains its primitive contour, the fascia dentata ending just behind the splenium of the corpus callosum. Hill,* not recognising the association between the disappearance of part of the hippocampus and the appearance of the corpus callosum, attributes this fact to "accident." But what happens in the macrosmatic mammal? For, in order to prepare for the advent of a corpus callosum, the whole of the upper and anterior part of the hippocampus has disappeared, and only the small temporal segment is left to carry on the functions of the whole. To compensate for this restriction, the hippocampus, as it grows, becomes bent upon itself in an S-shaped manner (fig. 6) and becomes accommodated *under* the corpus callosum, in which situation it may extend forwards almost as far as the foramen of Monro. This bending can be readily seen in the brain of the rabbit or fœtal pig. Hill, in discussing the question "whether the fascia dentata is continuous with the nervus Lancisii?" comes to the conclusion that there is no continuity between the two structures, and that the fascia dentata is essentially a *subcallosal* structure. His principal argument is that in the ox "he fails to see any indication of the return of the fascia dentata to the under-surface of the splenium in order that it may round the splenium and sweep forward in the nervus Lancisii in the manner required by the theory" [of Honegger and Zuckerkandl†]. This view, that the fascia dentata is essentially *subcallosal*, is not only directly opposed to the facts of its development as described and figured by Mihalkovics, Blumenau and Marchand, but also to the facts elicited by a comparison with the Marsupial. The corpus callosum occupies the same relative position to the Randbogen that the superior limb of the hippocampal commissure does in Metatheria, and hence the fascia dentata is essentially *supracallosal.*

If the suggestions concerning the striæ Lancisii advanced in this paper are correct—and the whole weight of comparative

* "The Hippocampus," *loc. cit.*

† *Loc. cit.*

and developmental facts, as well as the histological structure as described by Ramon y Cajal, seems to favour the view—then the cleft between the mesial stria and the callosal gyrus would be the anterior extremity of the Bogenfurche. So that for practical purposes the opinion of Schwalbe (which is essentially identical with those of Hertwig, Schmidt and Mihalkovics) that "the Bogenfurche in its upper part becomes the upper boundary of the corpus callosum" is for all practical purposes correct. Strictly speaking, however, the callosal fissure must be regarded as a new formation, because with the degenerate condition of the hippocampus is associated the practical absence of the "Ammonsfurche," the callosal fissure being formed by the growth of the cortex above the corpus callosum, causing it to bulge over the latter. So that Professor Cunningham's statement* must be regarded as strictly correct "that the Bogenfurche is transitory and is gradually obliterated during the time the corpus callosum assumes shape."

The facts brought forward in this paper afford a perfectly rational explanation of the circuitous course taken by the fornix fibres in the higher mammalia, without resorting to any such theory of the rotation of the brain as that advanced by Hill†—a pure speculation utterly opposed to all the facts of development. From an examination of the brain of a higher mammal, there is no apparent reason why the hippocampi should not be connected like the rest of the temporal lobe by the anterior commissure fibres. But just as by a comparison with the condition met with in the Prototheria, the reason for this is apparent, so also is the meaning for the course of the anterior pillars of the fornix above the foramen of Monro to reach the optic thalamus self-evident.

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* "The Surface Anatomy of the Primate Cerebrum" Cunningham Memoirs, Roy. Irish Acad. No. vii. 1892.

† Plan of the Central Nervous System, 1885.

EXPLANATION OF FIGURES.

Fig. 1.—Scheme of a sagittal section through the mesial wall of the cerebrum of *Perameles nasuta.* The alveus fibres represented in a purely diagrammatic manner.

Fig. 2.—Ditto. Platypus.

Fig. 3.—Ditto. Placental mammal.

Fig. 4.—Scheme of the hippocampus as seen in transverse section through the region of its commissures. The cells, axis-cylinders and collaterals shown as they are stained by Golgi's method.

Fig. 5.—Mesial view of "hippocampal region" in pig (fœtal) to show the S-shaped bend of the hippocampus; only the posterior part of the corpus callosum represented.

References to figures.

ac., anterior commissure; *af.*, anterior pillar of fornix; *alv.*, alveus; *c.*, "collateral" of an alveus fibre, ending in the *stratum radiatum; cc.*, corpus callosum; *d.*, molecular layer of the fascia dentata; *df.*, descending alveus fibres (to form the anterior pillar of fornix and the precommissural fibres); *ext. olf.*, external olfactory root; *f.*, fibres of alveus, represented schematically; FD., Fascia dentata; *fi.*, fimbria; *g.*, pyramidal cells of the hippocampus; *hf.*, hippocampal fissure; *hip.*, hippocampus; *int. caps.*, internal capsule lying in the corpus striatum; *l.*, bundle of collaterals (so-called superficial medullary lamina) derived from the pyramidal cells of the hippocampus, also transverse sections of bundles of longitudinally running fibres; M., foramen of Monro; *p.*, Purkinje-like cell of the fascia dentata; ps^1., dorsal limb of the hippocampal commissure; ps^2., ventral limb of the hippocampal commissure (the psalterium of placental mammals); *pyr.*, pyramidal cell of the subiculum cornu Ammonis; *rf.*, rhinal fissure; *s.*, precommissural fibres of the fornix-system; *sept.*, "septum pellucidum"; *s. hip.*, subiculum cornu Ammonis; *spl.*, splenium corporis callosi; spl^1., "*splenium of the hippocampal commissure.*"